THE VALIDITY AND INTERPRETATION OF INSECT FOODPLANT RECORDS

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SUMMARY

Literature records of insects and mites feeding on plants are examined in the light of experience in compiling information for the Phytophagous Insects Data Bank (PIDB). Data on *Senecio* are used to illustrate difficulties and uncertainties in the records, and the following points are reviewed briefly—species which are not fully phytophagous, introduced and migrant species, identification and nomenclature, unreliable data, geographic differences in food-plants, species in captivity, quantitative aspects of preference, and polyphagous species. It is concluded that food-plant data are still incomplete and that the objectives of studies using faunal lists are important in deciding on the most effective use of available data.

Introduction

Insect foodplant records are used to make lists of insects associated with particular plants for applied work and for research in ecology. Pests of agriculture, forestry and horticulture have long been considered in relation to their hosts, and nature conservation management is also now using foodplant data. Lists of insects appear in reference works on plant species as in the 'Biological floras of the Ecological Society'. Research into patterns in the interrelationships of insects and plants has increased since Southwood's (1961) classic paper on insects associated with British trees. For these studies also foodplant records provide a valuable and useful method of using accumulated information, often outside the capacity of an individual to collect (Kennedy & Southwood, 1984). However, details of the records used to produce lists of insects on plants are often rather vague, and close examination reveals difficulties in interpretation.

For some years, I have compiled insect foodplant records into the Phytophagous Insects Data Bank (PIDB), and have now reviewed all families of phytophagous insects and mites known to feed on higher plants (ferns to angiosperms) in Britain. During this work discrepancies in data on different insect groups and for different purposes have come to my attention. As many other workers also use or compile insect foodplant lists, it is thought that a summary of problems encountered in the compilation of records would be useful, and would provide a basis for any work with PIDB data.

DATA

The PIDB currently holds records of some 45 000 linkages between insects and plants compiled from the literature, from museum collections and from unpublished sources. This information is drawn upon for writing this paper. As an example, data for the genus *Senecio* have been summarized in Table 1. (The full data are available from the author.)

INSECTS TO BE INCLUDED ON FOODPLANT LISTS

Phytophagy and other feeding habits

Most phytophagous insects are clearly plant-feeding. However, in some species and groups phytophagy grades into other habits such as predation, omnivory, saphrophagy and myrmecophily. Lists of insects may be of plant-feeding species only as in Table 1, or may include all associated species.

Table 1. Summary of records of 137 species of British insects and one mite feeding on the genus Senecio (adult feeding excluded; plant nomenclature from Clapham, Tutin & Warburg (1962) or cited with authority).

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Plant species	Total insects	Mono- phagous species	Feeding on other plant families		onal infor Unreliabl data	
S. jacobaea †	72	8	30	5	3	1
S. vulgaris †	43	1	28	3	_	5
S. erucifolius †	12	_	2	1	_	_
S. aquaticus †	9	1	2	_	_	1
S. squalidus	8		2	1	_	_
S. viscosus †	5	_	1	2	_	
S. sylvaticus †	4	_	_	2	1	1
S. fluviatilis	2	_	_	3	_	_
S. paludosus †E	3	_	_	2	_	1
S. cruentus						
(Masson) DC. G	2	_		2	_	
S. doria	2	_	_	2		_
S. cordatus Koch	1	_		1	_	_
S. vernalis Waldst. & Kit.	. 1	_	_	1	_	_
S. cacaliaster Lam.	1	_	_	1	_	_
Other Senecio spp.						
(unnamed)	2	_	_	2	2	1
	22	(1)	•	11	2	1
Senecio records	22	(1)	5	11	2	1
(generic name only)						

[†] native species; E extinct?; G greenhouse species.

Some species are partially predatory, feeding on the plants and on prey species on the plants, e.g. Phytocoris and Psallus (Miridae). This habit may grade into fully predacious when the amount of plant material eaten is insignificant, but such details are not always known. However, some definitely predatory species are very closely attached to phytophagous prev which are specific to plants, and thus predators may be regarded as associated with particular plants although they are not feeding on the plant itself. These species can appear in foodplant lists e.g. Anthocoridae (Southwood & Leston, 1959) or Cucujidae (Walsh, 1954).

Omnivory may be the best definition of the feeding habits of some insects which can survive without feeding on plants but which nevertheless can be pests damaging crops e.g. adult carabid beetles attacking strawberries (Jones & Jones, 1974).

Saprophagy on rotting plants and dead plant materials is common, e.g. many Elateridae feed on dead and rotting wood; some Pyralidae feed on rotting leaves. Generally these species are not very specific to particular foodplants, and again their feeding habits may be poorly understood—they may be partially or entirely predatory. Other species are scavengers e.g. Limoniscus violaceus (Mull.) (Elateridae) (Leseigneur, 1972), and some may be associated with burrows made by other insects. Species feeding on stored products may not be easily categorized either, although they are clearly phytophagous.

Myrmecophily also occurs; the grade from phytophagy is well known in species of Lycaenidae; however myrmecophily is also found in aphids and Coccoidea, with similar intermediates of dependence on ants.

Another area causing difficulties over species to be included on lists is that of insects not actually feeding on higher plants, but on epiphytes like lichens or on associated fungi. Sometimes these species are listed for the higher plant rather than

their true host, which is more difficult to identify. This often occurs in species living on trees. Indeed in some groups all habits may be found in related species, e.g. in Anobiidae some species feed on wood, others on rotting wood and fungi, while some are definitely specific to fungal bodies (Lohse, 1969). On herbaceous plants, insects may be feeding on associated rusts or smuts e.g. Phalacridae or *Mycodiplosis* (Cecidomy-iidae).

Introduced species and migrants

Lists of insects on plants can include doubtfully British species, but there are problems in deciding which species have sustainable populations. Migrant Lepidoptera are recorded frequently, and some must obviously be included, but other

records may be based on only 1 or 2 occurrences of adults at light.

Like migrants, only a proportion of introduced species are fully established, and it is especially difficult to know how many of those feeding on plants in greenhouses and botanic gardens should be included. The problem is especially acute for Coccoidea, which are easily introduced on plant material, and where colonies may persist only as long as the foodplant, often in very small areas. Kloet & Hincks (1964) note species in this category with a distinguishing symbol.

LIFE CYCLE OF INSECTS AND RELATIONSHIP WITH FOODPLANTS

There are all degrees of dependence on plants by the different developmental stages in the life cycle of insects, so that the definition of a foodplant is not simple. I regard a true foodplant as a plant able to support the development of the insect from first instar larvae through to adult. This may be qualified to include as foodplants those species essential to a specific stage of development. e.g. early instars of the myrmecophile, *Maculinea arion* (L.) (Lycaenidae). Some records usually of smaller more immobile species may be excluded because although the food-plant supports more than one generation it does not sustain the species indefinitely (Westphal, 1980; Oetting, 1984).

There is confusion about the life-cycle stage listed for the foodplant in different insect groups. In Lepidoptera, it is currently customary to refer to plants for oviposition (Emmet, 1979; Heath & Emmet, 1979). Records of oviposition plant are usually the same as for larvae, so that selection by the adult of oviposition plants is regarded as most important. It is also relatively easy to observe Macrolepidoptera laying eggs, and to record the plants. However, not all species do in fact select the foodplant, but oviposit in nearby plants, leaving larvae to find the true foodplant e.g. Mellicta athalia Rott. (Nymphalidae; Warren, Thomas & Thomas, 1984). In groups, similar to Lepidoptera, where adults do not feed extensively, the larval foodplant is always recorded e.g. Tenthredinidae (Benson, 1958). However, larvae may move about, and can be recorded on plants other than those where development began. In extreme cases it becomes difficult to determine true foodplants. Soo Hoo, Coudriet & Vail (1984) showed that Trichoplusia ni Hübn. (Noctuidae) was only able to complete its full development on a limited range of plants when reared from the early instar. Later instars survived on a much wider plant range. This could occur in other polyphagous Lepidoptera, and may be a source of doubtful records, as it is common practice for collectors to take later instars, and rear these to adults, recording the plant on which they were found as the foodplant.

Species of many groups feed both in the immature stages and as adults on the same foodplant; this is especially obvious in the more immobile and gregarious species, like mites, aphids and scales. The difficulties of identifying larvae are greater than for adults, and in these groups larval feeding is ordinarily inferred from primarily adult

identification. Many Coleoptera also share the same foodplants for adults and larvae, but often these details are not given in the record, and adult beetles only are identified. It is more informative if both larval and adult foodplants are recorded, because in those species where good records are available, adults are often less specific than larvae, and have a wider foodplant spectrum for feeding than for oviposition, e.g. Curculionidae (Hoffmann, 1955–8) and Thysanoptera (Morison, 1947–9).

Adult foodplants can differ entirely from those of larvae, e.g. adults of nectar-feeding species, particularly Macrolepidoptera. Occasionally, adult feeding can be sufficiently important to confer pest status on species, e.g. *Phyllobius* and *Otiorhynchus* spp. (Curculionidae) have adults which can seriously damage foliage and flowers of fruit trees, while their larvae feed on the roots of these and other plants (Massee, 1954). For many purposes however, it is best to exclude these less specific adult feeding records as in Table 1. A higher total number of British records on *Senecio jacobaea* is given by Harper & Wood (1957) mainly because they have included species that do not breed on the plant, especially adult flower-visiting thrips.

Some insects have a life cycle in which different generations feed on different foodplant species or on different parts of the same plant. The obvious example is that of holocyclic aphids, which have entirely different summer and winter foodplants. Complications occur in those species which show facultative heteroecy or have regional anholocyclic forms e.g. *Metopolophium* (Aphididae) (Stroyan, 1982). Similar differences in foodplants between generations also occur in other groups, although less rigidly, and possibly related to seasonal availability of foodplants, e.g. *Eupteryx aurata* (Cicadellidae) (Stiling, 1980). Cynipidae have alternation of bisexual and agamic generations which cause galls on different parts of *Quercus*.

IDENTIFICATION AND NOMENCLATURE

Incomplete identification is especially common in foodplant records. Table 1 has 22 records for *Senecio* with no specific identification, and one of these is the only record. Where a generic name is given for a genus with only one native species in Britain, e.g. *Pinus*, it is likely that most records do refer to *P. sylvestris*. *Senecio* is less certain as both *S. jacobaea* and *S. vulgaris* are common species. Even less identity is supplied in some groups e.g. '*Carex* and Gramineae'. This is most frequent in plant groups where identification is more difficult for the non-botanist, and where it is harder to determine exactly which plant the insect was feeding on. Thus insect specificity appears to be less in Graminaea than in other groups, but this cannot be considered reliable until our knowledge of grass-feeding insects is more complete.

Sometimes only the English name for a plant is given and has to be interpreted to a standard Latin name. This causes uncertainty where more than one species is covered by the name. Ash is clearly *Fraxinus excelsior* in Britain, but 'thistles' might

be interpreted as Carduus and Cirsium spp.

Taxonomic status and knowledge of various groups differs. Plant species are very well known, but groups like eriophyid mites are taxonomically disordered. All taxonomy is changing to some extent, and data have to be continually revised. Lumping previously separate species is easily dealt with by additions, but splitting of a species causes all previous data to become unreliable. Checking names for synonym and correct spelling reveals numerous minor errors, becoming more serious when species appear under more than one name. Stille (1984) reduced the numbers of *Rosa* species galled by *Diplolepis rosae* (L.) (Cynipidae) from 20 to four due to synonymy. Misinterpretation of older records with synonymic changes has

produced errors which can be difficult to trace. Heath, Pollard & Thomas (1984) decided that, although *Viola canina* is cited as a foodplant for several fritillary butterflies, the dog violet proper is a rare heath species, and the name almost certainly refers now to the common *Viola riviniana*.

Use of signs of insect attack, such as galls or leaf mines, to identify species are specialized cases of possible confusion. Where a gall is clearly a recognizable structure, then insects or mites are quite often identified from this rather than the actual species inducing the gall (Bagnall & Harrison, 1928). Difficulties are especially acute for eriophyid mites, where species have been described entirely on gall morphology, e.g. *Eriophyes callunae* Swanton (Eriophyidae).

Finally, when computers are used for listing names, it is especially important to maintain accuracy in nomenclature. Checklists need to be consistent as errors caused by very small changes, e.g. dropping authority initials in the checklist of Auchenorhyncha (Le Quesne & Payne, 1981) as compared to the earlier edition of Kloet &

Hincks (1964).

UNRELIABLE DATA

There are quite a lot of unreliable data in the literature, e.g. for Senecio the PIDB holds seven unreliable records (Tables 1). Sometimes the questionable nature of the data is obvious because the author has said 'may be' a foodplant. At other times mistakes of identification have been made. Comparison of records shows up possible errors, for where genera or groups have species with reasonably closely-related foodplants, any entirely different foodplants may be wrong, e.g. a stenocephalid not feeding on Euphorbiaceae is likely to be an incorrect record (Schaefer & Mitchell, 1983). Sometimes the plants recorded as foodplants for an insect are taxonomically very different but grow in the same habitat, and more detailed investigation of the true larval foodplant is needed, e.g. Altica pusilla Duft. (Chrysomelidae) is currently recorded for Helianthemum, Poterium and Sanguisorba (B.N.K. Davis pers. comm.). Insects feeding on trees can drop off and be recorded as feeding on the plants below e.g. Coleophora serratella (L.) (Coleophoridae) (Coshan, 1974). Other unreliable records are of insects visiting plants, and recorded when probing or nibbling. Aphids in this situation are called 'vagrants' in some papers (Wood-Baker, 1979). Of course, some apparently incorrect records may be of genuine rare feeding, although whether such plants could support the whole life cycle may be unknown. There is an understandable tendency for authors to record foodplants that differ from the usual hosts. This is especially true of the many 'casual' records for Macrolepidoptera. These records have to continue in the literature until additional research shows that they are definitely unreliable or wrong.

GEOGRAPHICAL DIFFERENCES IN FOODPLANTS

The most important way in which British records are augmented is by comparison to continental European data, which may have the best foodplant lists currently available. This is such a common practice, that, at least in the past, it is not clear where these data have been used. Statements like 'male recorded twice in the Cairngorms, foodplant Betula' are suspect. For PIDB data in Table 1 there are quite high proportions of European records. Generally, European data reflect the potential foodplants of a species, and the probability that at some future time the same foodplant could be recorded for Britain. The same applies to world data on widespread species. Presumably more foodplants will be recorded with the possible plants in different countries, and this will be compounded in most data sets by the amount of effort made in compiling lists.

Some foodplant data may be primarily part of a taxonomic account of an insect group and no attempt made to specify the geographical location of records.

Local foodplant differences are known within the range of many species, e.g. the swallowtail butterfly, *Papilio machaon* L (Papilionidae) has a wide range of foodplants in the Umbelliferae (Berenbaum, 1981), but ssp. *britannicus* Seitz is confined to *Peucedanum* (Dempster, King & Lakhani, 1976). Lekander *et al.* (1977) found changes in foodplant with latitude for Scolytidae, e.g. the more northerly foodplants differed for *Dendroctonus*. Within the British Isles, Woodroffe (1971) thought that insects on the edge of their range in Scotland might have different foodplants. Regional specialization can occur when the spectrum of possible foodplants is incomplete in an area e.g. *Euura amerinae* (L.) (Tenthredinidae) occurs on *Salix pentandra*, but on *Populus* when *S. pentandra* is not available (Liston, 1982). The availability of foodplants differing locally may result in different choices of preferred foodplant by the more polyphagous species e.g. *Phalera bucephala* (L.) (Notodontidae) (West, 1982).

All grades of genetic adaptation to the foodplants of different geographical areas are found, from closely related insect genera and species to subspecies, races and populations. A few examples are cited here. Species of *Medicago* in different parts of europe have different species of *Sitona* (Curculionidae), formerly considered as local races of *Sitona humeralis* Steph. (Aeschlimann, 1984). Subspecies of *Eupithecia intricata* Zett. (Geometridae) differ within Britain; ssp. *arceuthata* Frey rarely feeds on native *Juniperus communis* in southern England, preferring ornamental Cupressaceae, while in the north ssp. *millieraria* Wnuk. does feed mainly on native *Juniperus* (Ward, 1977). Races of *Rhinocyllus conicus* Froel. (Curculionidae) feed on different Compositae in various parts of Europe (Zwölfer & Harris, 1984). Populations of the large bud moth, *Zeiraphera diniana* (Guenée) (Tortricidae) have different foodplants at different altitudes correlating with different colour forms in the larvae (Day, 1984).

SPECIES IN CAPTIVITY

Records of species and their foodplants in captivity are not uncommon in the literature. Usually these records are from tests for true foodplants; occasionally for giving advice on rearing when the wild foodplant is not easily obtained, e.g. Macrolepidoptera (Allen, 1949). Table 1 shows that the PIDB holds more captive records for *Senecio vulgaris* (groundsel)—a convenient plant to use for captive stock.

For studies of biological control of weeds using insects it is very important to test the potential foodplant range, and various choice tests or starvation tests with insects confined on possible hosts are used, e.g. Rhinocyllus conicus Froel. (Curculionidae) (Zwölfer & Harris, 1984). All degrees of survival may be recorded, and generally adults have wider potential feeding ranges than immature stages; older larvae survive on more foodplants than younger. Usually field records are for fewer foodplants than those found to be possible in captive rearing experiments. Quite often the insects are never found on plants available in the field, although they are successfully reared in the laboratory. Phenology may be important in some cases, e.g. Brewer & Skuhravy (1980) altered the emergence date of Monarthropalpus buxi (Laboul.) (Cecidomyiidae) which enabled this species to attack Buxus sempervirens var. bullata which had never been infested in the field because of lack of synchrony in development.

QUANTITATIVE ASPECTS OF FOODPLANT PREFERENCES

Some insect species are monophagous with all known records unequivocally for

one foodplant, particularly where the foodplant genus is itself monotypic. Data on *Senecio jacobaea* give eight out of 72 species currently recorded only from this plant, while *S. vulgaris* and *S. aquaticus* have one monophagous species each (Table 1). I believe that many monophagous species will eventually be recorded attacking other plants in the same genus.

Most records are samples from populations of insects attacking populations of several possible foodplant species. The resulting quantitative data on preferences cannot be clearly defined except under controlled experimental conditions, although obviously some species are important hosts and others rare. A method which is commonly used for testing foodplant range and preference in the field is the provision of a series of potential foodplants for natural colonization, e.g. cruciferous plants attacked by the swede midge, *Contarinia nasturtii* (Kieff.) (Cecidomyiidae) (Stokes, 1953). Botanic gardens with good plant collections are also useful for preference testing (Davis, 1982). Field methods are often used in conjunction with captive resistance and starvation tests.

Insect abundance

Population sizes of insects are not the same in different years, and this may influence the numbers of foodplant species recorded. Euproctis chrysorrhoea L. (Lymantriidae) has a sequence of foodplants; the preferred plant, Hippophaë rhamnoides has the highest attack rate, and increasing numbers of additional woody plant species are attacked as the populations rise (Voute & van der Lind, 1963). Similar data have been noted briefly for Thecodiplosis brachyntera (Schwag.) (Cecidomyiidae) which attacks more Pinus species at higher population levels (Brewer, Skuhravy & Skuhrava, 1984).

Plant abundance

Common plants have more insects than rare plants (Strong, Lawton & Southwood, 1984). These commoner species normally cover a wider geographical area and have had greater recording effort. Economically important plants are especially prone to these effects; Schaefer & Mitchell (1983) note that there are many spurious references to monophagous feeding on cocoa and pigeon pea for Coreinae (Heteroptera). Entomologists report more details for economic plants, e.g. 'causes damage to lettuce and other plants'. Conversely the status of insects on rare plants, especially some herbs, is often poorly known because entomologists have traditionally been more concerned with the collection and taxonomy of the insects, than their foodplant spectrum, and have not been likely to search out rare foodplants or plants with identification difficulties. The common Senecio jacobaea has records of 72 species and S. vulgaris has 43, while the less common species have far fewer records, and nine rare or introduced species of Senecio in Britain have no records (Table 1). These data are certainly incomplete, and for example, Smith (1979) has recorded two unidentified species on Senecio integrifolius, which otherwise has no records.

POLYPHAGOUS SPECIES

There is no exact definition of a polyphagous species, but, as generally understood, it is an insect feeding on a number of unrelated plants. Schaefer & Mitchell (1983) for example, decided that a polyphagous species fed on more than five plant families; but that out of 219 species of Coreinae only 45 could be reliably assigned to either mono-or poly-phagy because of various uncertainties. Indications of the likely proportions of insects on *Senecio* which are not restricted to Compositae are provided by records of alternative hosts in other plant families (Table 1). These

account for nearly half the records for S. jacobaea and more than half on S. vulgaris.

For most, if not all, polyphagous species the numbers of foodplants given in the literature are likely to be underestimates. Börner (1952) lists 184 foodplants for the summer morph of *Myzus persicae* (Sulz.) (Aphididae), while the world slide collection in the British Museum (Natural History) produced 196 hosts for *Coccus hesperidum* L. (Coccidae). These lists are definitely incomplete.

A well-known difficulty with polyphagous species is that of very long lists of foodplants. In many cases only a few foodplants are noted, usually common or economic plants, followed by remarks such as 'and on many other plants'. One solution is to at least list plant families or higher groups attacked, as in Eastop (1981) to show the range of plants attacked. Many polyphagous species do have restrictions and do not feed on certain plant families, e.g. Cerambycidae are often more or less restricted to either Gymnosperms or Angiosperms (Duffy, 1953).

DISCUSSION

The study of insect foodplant records is an important way of using accumulated knowledge. However, the various difficulties outlined above mean that lists of insects feeding on particular plant species are subject to some uncertainties with present data. Additionally, objectives for the use of lists must be taken into account

in their compilation.

There is definitely some bias in literature records, because of the emphasis on commoner or economic insects and plants and the failure to record all hosts of polyphagous species. In a comparison of field and literature data, Niemela & Neuvonen (1983) were easily able to add to the list for Macrolepidoptera on rarer trees in Finland. They thought that the geographical effect of species richness was overestimated because of incomplete recording of polyphagous species on rarer hosts. Britain is one of the best studied areas in the world, but even here new foodplant records are continuously made and species of phytophagous insects new to the country or to science are added. As this information accumulates lists are extended; better literature searches are made, and total numbers for particular plants increase. For example, Southwood (1961) listed 91 species for *Pinus sylvestris* in Britain, and in Kennedy & Southwood (1984) increased this to 172. PIDB data has a similar number of 173 British records for *Pinus*, but the potential is obviously higher as there are 238 British species when continental European foodplant records are included.

It is important to decide on objectives when using faunal lists for plants. Data on stenophagous or monophagous species are more relevant to many ecological studies, and some 50% of insect species are restricted to one plant family in the PIDB records. The many casual feeding records of polyphagous species may be confusing and could be omitted. However, for taxonomic studies of the insect species all available data on foodplants may be relevant. For biological control of weeds, knowledge of host specificity is important in preventing attacks on related crop plants, and data will include laboratory records of preferences. In evolutionary studies the interplay of field factors may be more important, and records of potential foodplants from captive data might be excluded. Similarly, where total dependence of species on plants is important, larval but not adult foodplants should be used. In work on biogeography, lists compiled using political areas produce bias and are unsuitable for some studies (Kuris, Blaustein & Alio, 1980). The distribution of some introduced species has not reached equilibrium, and Ward & Lakhani (1977) thought that introduced insect species should be excluded from studies of foodplant island sites of native juniper.

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